IMPERIAL BUREAU OF FRUIT PRODUCTION

TECHNICAL COMMUNICATION No. 5

THE "DEGENERATION" OF THE STRAWBERRY

Part I.—The pomological aspect. *By* D. Akenhead, M.A., B.Sc.
Part II.—Virus. *By* R. V. Harris, B.Sc., A.R.C.Sc., D.I.C.
Part III.—Root Rot. *By* G. H. Berkeley, M.A., Ph.D.
Part IV.—Insects and other animals. *By* A. M. Massee, F.R.E.S.
With a foreword by B. T. P. Barker, M.A.

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I. The pomological aspect of strawberry degeneration. *By* D. Akenhead, Imperial Bureau of Fruit Production, East Malling, Kent, England.

II. Virus as one cause of strawberry degeneration. *By* R. V. Harris, East Malling Research Station, Kent, England.

III. The phenomenon of root rots in connection with strawberry degeneration. *By* G. H. Berkeley, Senior Pathologist in Charge, Laboratory of Plant Pathology, St. Catharines, Ontario, Canada.

IV. The insects and other animals associated with degeneration of the strawberry. *By* A. M. Massee, East Malling Research Station, Kent, England.

With a foreword by B. T. P. Barker, Director of the Agricultural and Horticultural Research Station, Long Ashton, Bristol.

Price 2/-

February, 1934.

FOREWORD

Throughout the past two decades no kind of hardy fruit has proved more difficult to grow successfully under commercial conditions in the North Temperate Zone than the strawberry. From many widely separated areas in both Europe and North America the " degeneration " of the plants has been reported repeatedly, and accounts of fresh failures appear frequently. The liability to breakdown under culture seems to be of practically universal distribution. During that period this fruit has probably been subjected to more extended pathological research than any other of the soft fruits. Although many workers have attacked its problem in this direction, the fact that no royal road to success can yet be indicated with confidence to growers suggests that much further investigation still is required on what has proved to be a most complex issue.

Under such circumstances the following Technical Communication on Strawberry Degeneration, with its comprehensive survey of the researches on these problems, will be found valuable to all interested in the subject. To individual workers desiring to view it from angles other than those with which they are immediately concerned, a review of this kind should prove of particular service. The Communication is issued by the Imperial Bureau of Fruit Production. In its compilation the co-operation of pathologists has been enlisted, owing to the complexity of the problems and the varied pathological aspects associated with the symptoms of degeneration. The latter suggests the trouble as striking deeper than cultural defects remediable entirely by treatment upon purely pomological lines. Such advances as have been made already are due largely to the recognition at an early stage of the necessity for team work by investigators concurrently engaged on the main problem and attacking it from the points of view of the pomologist, the plant physiologist and the pathologist. Owing to the latter aspect, Sir Guy Marshall and Dr. E. J. Butler, the Directors of the Imperial Institutes of Entomology and Mycology respectively, have been consulted, and their approval secured for the inclusion of the sections on those subjects. Acknowledgment is due to them for their critical aid in respect of those sections and for material assistance in their improvement.

This Technical Communication is composed of four distinct contributions, dealing respectively with the pomological, virus, root rot, and entomological aspects of degeneration. It is difficult on reading each in turn to resist the conclusion that under each head sufficient cause for widespread trouble in the culture of this fruit has been indicated. Notwithstanding this, many associated with strawberry-growing in this country as it was before the War may be tempted to compare conditions and results before and since and enquire why, with far less knowledge and practice of methods of disease and pest control in those earlier days, it appears far more difficult now than then to maintain a bed of plants in vigorous condition and full cropping capacity throughout its normal lifetime. Even in cases where beds apparently thrive for the first year or two of their lives it is unusual at the present time to find any not showing wholesale deterioration in the later stages. Has some radical weakening change in the constitution of the strawberry plant developed in recent times ?

Bearing upon that question, so far as this country is concerned, the possible effect of cultural conditions during the war period may be significant. At that time it became necessary to produce crops of higher food value than the strawberry, and for a few years in succession commercial growers were not permitted to plant new beds. When in due course fresh plantings were sanctioned, a great demand for runners arose immediately, the supplies of fruit by that time having fallen far below normal requirements. Consequently, a situation was created in which runners were taken without discrimination from parent plants, totally inadequate in number to provide the required supplies, and thoroughly unsuitable in age and vigour for the purpose. In many cases, even divided old crowns were planted out, owing to lack of runners.

Under such circumstances it was inevitable that the quality of the strawberry beds in the period immediately following the war years should be inferior generally to the average level of those existing before the outbreak of war.

Nevertheless, having regard to what has happened in other directions in horticulture, thanks to the skill of growers, it might reasonably have been expected that by the present time an approximation to pre-war standards of quality would have been reached at the least. If one can judge from the expressed opinions of those in a position to make comparisons, that stage has not yet been achieved in general practice. Moreover, the failure has occurred in spite of the concerted efforts to effect improvement made possible by the scheme of certification of strawberry runners organized in 1927 by the Ministry of Agriculture and Fisheries. Under that scheme there have become available for growers extensive supplies of runners certified in respect of general health and quality.

Notwithstanding this unsatisfactory position, it may be premature to conclude that the degeneration is definitely associated with even a temporary constitutional change in the plant. The writer has in mind certain plots on which successive beds of strawberries have been grown continuously over a nine-year period : on the best of these a four-ton per acre yield was obtained in 1932. Even if judged by pre-war standards, this result must be accounted good. It would seem to indicate that, provided care is taken in the selection of runners for planting, the cultural and nutritional treatment of the beds, and the application of appropriate methods of control against diseases and pests, a high standard of performance can be secured under circumstances where local conditions are not specially favourable. It is unquestionable, however, that without that care and without consideration of many of the investigations which are reviewed in the following pages, a result of that degree of success would not have been attained.

Thus, although admittedly the problems associated with the degeneration of the strawberry are still apparently far from being completely elucidated, and a great task lies ahead before the culture of this fruit is restored to a satisfactory basis throughout the world, it would seem that application of the knowledge already resulting from the intensive research on the subject can aid the grower greatly. By the collection of the available information and its presentation in this Technical Communication in so concise and handy a form, the Imperial Bureau of Fruit Production has merited the thanks of growers and investigators alike.

B. T. P. Barker,
Director,
University of Bristol,
Department of Agriculture and Horticulture,
Long Ashton, Bristol.

17th January, 1934.

The Bureau wishes to thank Mr. R. V. Harris, Dr. G. H. Berkeley and Mr. A. M. Massee for their valuable contributions, and to convey to Professor B. T. P. Barker their appreciation of the help which he so readily gave in reading the completed memorandum and providing the foreword.

I. THE POMOLOGICAL ASPECT OF STRAWBERRY DEGENERATION

By D. Akenhead, Imperial Bureau of Fruit Production.

The problem of so-called strawberry degeneration is not a simple one to be solved entirely either by the mycologist or the entomologist, or indeed by the pomologist alone.

In the report of a recent conference on strawberry investigations by the American Bureaux of Chemistry and Soils, Entomology and Plant Industry, the U.S. Department of Agriculture and the North Carolina Agricultural Station, the following conclusion is reached. " The causes of dying of strawberry plants may be attributed to many factors including the following :— drought, insect injury, high soil temperatures, soil acidity, fertilizers, root diseases, strawberry dwarf, leaf spot diseases and improper tillage and cultivation."

It is therefore proposed to consider certain of the more important factors, which quite apart from any question of disease or pest may have profound influence on the production and life of the strawberry.

Varieties.

The fact that strawberry degeneration has been noted in all strawberry growing countries, where entirely different varieties are grown, suggests that, although certain varieties are more susceptible to environment, to pest attack or to disease than others, a simple remedy cannot be provided merely by the selection of hardy varieties.

Strain.

Lack of care in selecting parent plants from which to propagate has certainly been responsible for considerable loss in the strawberry fields. A note on " Blindness " (1) in strawberry plants occurs in the Journal of the Ministry of Agriculture, vol. 29, No. 87, 1922. We read : "Blindness is easily recognizable by the presence of strong growing, luxuriant, foliage producing plants which do not flower. These in turn produce strong, healthy runners, which are as a rule more robust than those produced by plants having a normal crop. The runners of such plants seldom produce fruitful stools, but show a marked tendency to produce abnormal foliage and no flower. . . . It is generally agreed that certain varieties of strawberries have a tendency to throw more barren plants than others, and although they appear under the best soil and manurial conditions, it is also possible that poor cultural conditions have some effect in their production." The advice is given that only runners from fruitful plants should be selected for propagation.

The theory, however, that runners from " blind " plants will not produce fruit satisfactorily has now been largely refuted by Ball (4) and Rogers (29), both of whom studied runners from parent plants which failed to fruit in the first year. They found that the great majority of these runners fruited normally. Ball concluded that apart from the question of possible sterile " rogue plants," lack of fruiting is generally due to lack of vigour.

Refusal to crop satisfactorily by certain varieties which normally crop heavily has been investigated on more than one occasion. Most of the work in this country on the subject has been done at Long Ashton, where a series of investigations was made on different strains of Royal Sovereign (20, 32).

In 1915 Barker (9) reported that results " show as a whole unexpectedly large differences between the individual strains, the Jersey plants being far ahead in both seasons. But even if this be considered an abnormal case, there still remain relatively large and important differences in the others." The Royal Sovereigns in question came from 12 sources.

In 1925 Ball (3) spoke of the different cropping powers shown by various strains under examination at Long Ashton and suggested 4 possible causes :—(1) the existence of pure lines, in which case selection should be made for heavily cropping lines, (2) simple differences in vigour due to environment, (3) health of plants and (4) presence of a large proportion of rogues, which implies the necessity for careful rogueing of the parent runner beds.

Results of later work at Long Ashton (20) reported in the Annual Report for 1927 did not entirely confirm these conclusions. Results were noted on 4 generations of 7 strains. One strain in particular gave consistently good results throughout. The remaining strains were at first sight noticeable mainly for their inconsistency, though on a closer examination some at least of these inconsistencies seemed capable of explanation.

In 1928 Staniland (31) published a survey of strawberry plantations in England. In it he states :—" In all districts visited stocks were seen, which were very mixed. ' Rogues ' consisted of other commercial varieties and of ' wild plants.' The latter may be non-fruiting or productive of very bad-flavoured fruit. Some of them produce very large numbers of runners, and, if care is not taken in rogueing, the percentage of wild plants increases very rapidly." He recommends that growers should be particularly careful to replace weak stocks by duly certified, strong, healthy stocks.

Whether many so-called strains are inherently different or merely different as the result of present or past environment or cultivation practice, etc., is not always clearly determined. Thus Ball (4) concludes that strong parents yield more strong progeny than do those of moderate vigour, and those of moderate vigour than those that are weak. This does not necessarily mean, he adds, that there is any genetical difference between a strong and a weak parent, for vigorous parents throw more runners and begin runner production earlier than do weak ones. Rogers in 1930 (29) discussing 3 years' records of experiments laid out on statistical lines at East Malling, reports that three strains of Royal Sovereign, which in the first generation showed significant differences, were made much more uniform in the two following generations by the elimination of weak and unhealthy plants and by the selection of vigorous runners. Since this report was published we learn that the plantation in question has been attacked by " strawberry yellow-edge " virus and that one particular strain has been obviously more resistant than the others.

But whether the cause of the differences observed between plants of the same variety is to be sought in genetic composition or in past environment, the moral remains unaltered, namely that it is imperative to select from healthy, normal parent plants, which show no signs of exhaustion from fruiting or excessive runner production or from any other cause whatever. One of the essential conditions to success as noted by Wardlaw (41) is a good stock of plants, well selected and rogued and well suited to the type of soil.

Runners.

A cause of debility and " running out " in the strawberry plant is careless preparation and selection of runners (28, 32). Ball (3) has devoted considerable attention to the problem and in 1925 he recommended :—(1) The elimination of all " rogues " and diseased plants from the runner bed. (2) A restriction of the number of runners allowed to remain on a plant. (3) Restriction of selection of runners to a special bed of maiden plants, which can be carefully selected and rogued for diseased plants and plants not true to name.

A year later (4) he confirmed these views and was further able to note that restriction of the number of runners formed increased the vigour of the progeny.

The formation of runners is an exhausting process. Darrow (13) in the *Journal of Agricultural Research* for 1930 reports as follows :—In 1925-26 in Maryland the limiting factor in growth was temperature. The vigour of the parent plant was greatly increased by the removal of runners

as they appeared. A comparison between the mean daily increment values of total leaf product for the same plant showed that for plants from which runners were removed these values were all positive although fluctuating greatly, whereas for plants producing runners they were usually much smaller, and were actually negative, indicating a net loss for 3 of the 17 periods.

Experience in New Zealand (26) is the same, and the recommendation is made that plants should not be allowed to make runners until main crop fruiting is over.

Staniland (31) in his survey of the strawberry plantations of England makes the following points :—Another important cause of the weakening of stocks is undoubtedly the lack of care taken in the selection of runners. It is much better to take limited first runners from deblossomed maiden plants after thoroughly rogueing parents at flowering time, than to allow unlimited runners to root from fruited maidens. In consistently dry years it is unwise to take runners from plants whose vigour has been thus impaired.

To maintain healthy stocks he considers it essential to give special attention to the following points :—

(1) Enough maiden plants should be set aside as parents.

(2) These should be rogued for disease or abnormality or weakness.

(3) They should be deblossomed.

(4) Not more than 5 runners should be allowed per parent. They should be stopped after the first runner plant has formed. Succeeding runners should be removed.

Rogers' (29) work at East Malling has confirmed the value of deblossoming plants from which runners are to be taken. He reports that in every case the deblossomed plants had a considerably larger weight of runners than the fruiting plants, amounting to an over all increase of 32%. Further he concludes that from the point of view of runner production it is quite clear that early planting and deblossoming of the parent plant are of great value.

In later experiments at East Malling all the runners formed by selected parent plants have been planted out and recorded individually for vigour, cropping and disease.* We are informed that the work has shown that early formed runners initially give larger plants, and more blossom in the first year than late formed runners. On deblossoming these plants, however, indications were given that the size of plant evens up very greatly, so that in the second year there is little difference in size of plants between early and late formed runners. The amount of fruit borne per plant in the second year is also very similar. Even the smallest runner produced good plants under these conditions.

Fertility and Sterility.

A factor sometimes disregarded is the varying flower formation in the strawberry (11, 25, 30, 36). Some strawberry varieties have perfect flowers, while others produce only staminate flowers. Although this factor may be traced to the ancestors of the cultivated strawberry, it would appear to have been fairly often disregarded, with the result that pure stands of the imperfect-flowered varieties have been planted from time to time and have consequently produced very poor, negligible crops. Thus during the last decades extensive plantings have been made in England of the Oberschlesien and Tardive de Leopold varieties owing to their vigorous growth and resistence to disease and to the strawberry aphis. Tardive de Leopold is actually known to be completely self-sterile, but presumably—if the factor of sterility was considered at all—it was expected that Oberschlesien would prove an adequate pollinator. Accordingly the two varieties were planted close together in the absence of other varieties and

* A note of this work is given in the *East Malling Research Station Annual Report* for 1932, 1933. A. 16, page 33.

crop failure resulted. The reason has now been determined by Swarbrick and Thompson (33) as the complete absence of pollen in Tardive de Leopold combined with lack of viability and vigour in the pollen of Oberschlesien. Interplanting with such a vigorous pollinating variety as Royal Sovereign is found to cure the trouble.

In all cases where sterility or inefficient pollination is suspected, interplanting with a perfect variety is essential.

Climate.

Darrow has found that climate may affect sterility. In 1927 (11) he writes :—" Evidence that sex expression in hermaphrodite varieties is changed by soil conditions has been obtained by others and apparently is confirmed. The character of the fall season is considered one of the important causes of fertility and sterility in this fruit." Further Darrow (11) showed that also in the growth of strawberry plants temperature may be the limiting factor. There is also evidence that strawberry crop failures are in some cases due to drought. Bunyard writes in 1931 (10) in the *Gardeners' Chronicle* :—" Would it be well to revive the old custom of mulching beds with straw in autumn to retain moisture and keep out frost ? " Failure due to drought is confirmed by other correspondents.

In England, at any rate, a very good case has been made out for early planting. Mann and Ball (7) sum up as follows :—Experiments made very strikingly indicate the necessity for " planting runners at the earliest possible date compatible with local conditions. The earlier the runners are in their permanent quarters, the more likely are they to make strong crowns, since they are able to make full use of the latter portion of the normal period of shoot development. This increased crown development further ensures vigorous new root formation, and consequently less loss of plants will be experienced." At Long Ashton, in Western England, with a heavy rainfall, August planting was much more successful than September. At East Malling (29), however, which is in South Eastern England and has a much lower rainfall, August was found definitely too early, though even here early autumn gave much better results than winter or spring planting. In Canada dry spells in the autumn result in spring planting being more generally adopted (23, 28).

Cultivation.

Gleed (17), dealing with work done and observations made at the Botley fruit station in Hampshire, writes as follows :—" As to the symptoms of the various strawberry troubles, any factor causing a check to the plant's growth seems capable of producing much the same type of symptoms, and it is not easy to decide whether dwarfed growth, small leaves, a poor root system or general debility is due to poor cultural treatment or soil conditions, weather or poor stock, or is the result of attack by one or more of the insects or pests to which strawberries are subject."

The strawberry beds at Wisley show the excellent results of proper cultivation methods. Admittedly results are of the before and after type and controls are absent. Yet improvement is manifest, so much so indeed, that Forsyth (15), describing the work there, states that Mr. A. N. Rawes has, during the course of the past 5 years, so improved the stocks of the older varieties included in the trial that all signs of ill-health so prevalent throughout the country have now disappeared and the varieties have been brought back to their former vigorous condition, thus confounding the view that the old standard varieties were " run out " and of no more value. This rejuvenation, he writes, has undoubtedly been brought about solely as a result of correct cultivation, the timely application of fertilizers, lime-sulphur spraying for the control of mite, etc., combined with careful selection when propagating. At Wisley no more than 4 runners are taken from each plant and only healthy plants are selected for perpetuation.

Facts which must be taken into consideration are the time and place of root formation in the strawberry. Mann and Ball (22), in their second study of root and shoot growth in the strawberry, write :—" The chief point recorded is the time of root activity, the main roots being formed in the late summer and autumn. The new main roots arise at a higher level than the older ones. Thus the value of maintaining close contact between soil and crown soon after cropping may again be emphasized. In addition the fact that the plant depends in the following season very largely on the roots formed in the period extending from shortly after the cropping season until the early winter indicates the value of assisting this root growth by every possible means. The progress made by the plant in forming strong, healthy roots and crowns in the season immediately after cropping is of the utmost importance." They were able to make the further observation from later trials that earthing up in August increased the vigour of plants. Further (6) in their review of Long Ashton investigations they made the following among other suggestions :—Clean and cultivate just after cropping and encourage root growth at this season, e.g., by maintaining close contact between soil and crown. Slight earthing up they consider to be decidedly advantageous, as it increases the chances of vigorous root production.

These conclusions are supported by the editor of the *Gardeners' Chronicle* (16), who adds also a plea for the application of a fertilizer containing P and N prior to earthing up and for a short delay of 2-3 weeks to give rest between cropping and cleaning the strawberry plant. Middleton (24), commenting on these suggestions, writes as follows :—" . . . its habit of producing new roots above the old is inherited from its woodland ancestors, which are annually half buried in a layer of decaying leaves that provide an excellent rooting medium. It seems to follow that the correct treatment would be to apply a good mulch in August, largely composed of leaf soil and packed well round the crowns. . . . The critical point is during dry periods in late summer, when it is left to struggle on as best it may." He suggests that a complete rest during which it is allowed to form runners and go wild allows it to recuperate and regain its old health.

As regards ordinary routine cultivation practice Wardlaw (41) recommends (1) It is absolutely essential to have deep and thorough cultivation, thorough drainage and a fine friable tilth. (2) The plough pan must be broken and the subsoil well stirred. (3) Where a wet area occurs, it is advisable to set the plants on drills at that point so as to give the roots a better chance of avoiding rotting. (4) Tilth must be good, otherwise bad rooting will take place and disease appear if weather is unfavourable. (5) Tilth must be kept good.

Waterlogging.

Adequate drainage is essential and waterlogging must be avoided.

Mann and Ball (8) made particular note of its effects on plant growth and found that they were greatest on size and colour of leaves. After experimental subjection to waterlogging for some time the new leaves produced never attained normal size, but remained very small, resembling in size and shape those produced by extreme exposure of the crowns (i.e., as when earthing up is omitted). The older leaves assumed autumn tints very early and died abnormally soon, and as a result of their death and of much of the root system, the new crowns were very weak and produced abnormally small leaves. The remedy suggested is furrowing in autumn between the rows.

Mechanical Damage.

The same workers (8) investigated the effect of mechanical damage both to crowns and roots caused by faulty methods of cultivation. As regards the former they found that it resulted in " small leaf " symptoms, which normally, other things being equal, disappear in course of time. Damage to roots, on the other hand, in the spring or summer resulted in decreased vigour. The size of leaves was also smaller and they approached the condition of those borne on plants with raised or exposed crowns.

Manuring.

Adequate manuring is essential not only for crop production but for the health of the plant. Antoshin (2) after discussing the varied and somewhat contradictory results of research work, comes to the conclusion that strawberries seem actually less prone to react to mineral fertilizers than other fruits, the lack of favourable reaction noted being probably due in some cases to the previous application of organic manure and sometimes to faulty application resulting in leaf damage. It would appear that N deficiency has the greatest effect on growth followed by P deficiency, K not being so important. Important work on the effect of fertilizer application on fruit bud formation has been done in Canada and U.S.A. (14, 18, 43) which confirms the results of Wallace's deficiency studies in England (37, 38, 39, 40). The question of liming is still unsettled. While strawberries would appear to tolerate a somewhat acid reaction, the addition of lime after the application of acid fertilizers has sometimes been extremely advantageous (2). A balanced fertilizer (26) would seem essential as also the maintenance of proper soil aeration by suitable methods of cultivation.

Considerable light is thrown on the question of manuring by recent investigations in North Carolina. Lineberry (27) here reports that the organic matter content of soils, the reaction of soils and a high soluble salt content are factors of the greatest importance to the life of the strawberry. Comparison, he writes, of the organic matter of soil samples from a large number of spots in fields containing good plants with those containing poor plants showed the organic matter higher in the case of thrifty plants in 95% of cases examined. No close correlation was found between the pH of soils and the viability of plants, though an extremely low pH, i.e., high acidity, was generally associated with low viability. Moreover large amounts of water soluble salts in the soils within the root zone of the plants, resulting from the addition of fertilizers, was unfavourable to the viability of strawberry plants.

Cultivation methods, pollination, soil and other environmental conditions all exercise a profound influence on the life and health of the strawberry. Hence, before seeking to determine the identity of some finally destructive pest, disease or virus it would seem desirable to ensure that the plant is not merely suffering as the result of faulty methods of cultivation, poor soil or neglect of some elementary precaution. Hodson (19), in his paper on strawberry pests, urges that such a determination shall be the first consideration. Thomas's note (35) in *Phytopathology* a few years ago confirms this view. In his investigations of the causes of the killing of strawberry roots he made many unsuccessful attempts to produce disease symptoms in strawberries by inoculations with known pathogenes taken from the roots of diseased or dead plants, nor were his other attempts to induce disease in healthy plants by the juxtaposition of dead plants or of supposedly infected material any more successful. He therefore concluded that root killing in New York State may result from a number of causes frequently in combination, and that fungi in most cases at least play a minor rôle. In his opinion strawberry plants are notably sensitive to soil and other environmental conditions. Factors which seem particularly to influence the occurrence of root killing are :—type and exposure of soil, low temperatures, application of lime, mulching.

The writer is much indebted to Mr. W. S. Rogers for his constructive criticism of these few notes.

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II. VIRUS AS ONE CAUSE OF STRAWBERRY DEGENERATION.*

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1. Introduction.

In recent years strawberry growers have experienced very great difficulty in obtaining good and uniform performance from their strawberry plants. It is common knowledge that the stocks of certain widely grown varieties (e.g., Stirling Castle and Royal Sovereign) have degenerated. An examination of almost any commercial plantation of such varieties will show that there is a very considerable variation in behaviour from plant to plant. The determination of the causes of this has been approached from various angles in attempts to arrive at a practical remedy. Some investigators have studied the part played by mite and insect pests commonly associated with degenerate plants. Other workers have placed the emphasis on defective soil and cultivation conditions combined with the action of parasitic organisms, whilst others have concluded that in certain cases the primary cause is a virus inherent in the degenerate plants and transmitted to their runner progeny.

A recent investigation of Royal Sovereign " strains " at East Malling (38) revealed the fact that, while runner selection and the control of the strawberry mite eliminated a certain amount of variation, loss of vigour followed by death could still be observed in the field (46). It was then decided to test for the possible presence of a virus in such cases of " degeneration." In order to obviate the masking of virus symptoms by the artificial infestation of plants with suspected mite and insect vectors, grafting methods of transmission were devised and applied, and a disease of this nature was finally identified (44, 45). The discovery of this virus disease has thrown considerable light on the nature of the strain variation in Royal Sovereign recorded both in the original trial plots and in subsequently elaborated field experiments at East Malling (see p. 14), and it is already clear that infected plants must be eradicated or reduced to negligible proportions, if any degree of uniformity in plant performance is to be secured.

2. American literature.

Horne (1) in 1922 was the first worker to identify and describe the symptoms of a serious degeneration disease of strawberries occurring in California. A detailed study of this disease was subsequently made by Plakidas, who in his preliminary paper (2) referred to the disease as " Strawberry Yellows." In a later paper (4) he changed the name to " Xanthosis " and described a large series of infection experiments, from the results of which he concluded that the disease was caused by a virus. In these experiments successful transmission was only effected by using the aphis *Myzus fragaefolii* as a vector. The symptoms described by Plakidas correspond very closely to those of the " Yellow-edge " disease in England. (45) Briton-Jones and Staniland (30) also drew attention to the similarity between the symptoms of Xanthosis and those of "Aphis-plant " (*Capitophorus fragariae*) in England.

In 1928 Plakidas (8) described another degeneration disease occurring in the Southern States, which he referred to as " Strawberry-dwarf " and which he considered to be distinct from the Yellows or Xanthosis of California. He suggested that this might be another disease of the virus type and described transmission experiments with an aphid (probably *A. forbesi*), which yielded positive results, although the units used were not sufficiently large for a final conclusion to be drawn.

Brooks in 1930 and 1931 (16) and Stevens and Mook (15) in 1930 differed from Plakidas as to the origin of Strawberry-dwarf (called " Crimp " by Brooks in Florida but identified by him as the same as Dwarf) and concluded that it was caused by eelworm.

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* This article is not entirely as received from the author. Shortly after its receipt, when Mr. Harris had left for a year at St. Catharine's, Ontario, it was decided to enlarge the scope of the memorandum and to include other aspects of the strawberry problem. Mr. Harris kindly consented to the necessary adjustments being made to his paper by the Bureau, and for such adjustments the Bureau is responsible.

In 1927 Berkeley (5) working at St. Catharine's, Ontario, Canada, first reported and described in some detail the occurrence of a " mosaic-like " disease of strawberries. He pointed out that certain characteristics of this disease suggested " virus," while others indicated the possibility of it being genetic in origin. In 1928 Berkeley (6) again reported on this disease to the effect that some 200 inoculations gave negative results and that further experimentation was necessary to ascertain the true nature of the trouble.

In 1930 Berkeley (7) reported the results of further inoculation tests, all of which were likewise negative. Evidence was submitted at this time to show that the disease was seed borne. As to the nature of the trouble, Berkeley stated that " although the symptoms are very much like those associated with mosaic disease, nevertheless, there are differences which cast some doubt upon this being a true mosaic trouble. The possibility of it being a genetic trouble is not to be overlooked."

In 1929 Plakidas (9) published a brief note on this same disease and suggested that it be called " yellows " to differentiate it from xanthosis. In 1932 (10) he suggested the name " June Yellows " because, as he says, the "symptoms are more pronounced in early summer." He also recorded that " all attempts, however, to transmit June yellows by juice inoculations and leaf mutilation, by use of soil, by insects [whiteflies, leaf hoppers, and aphids (*Aphis forbesi* and *Capitophorus fragaefolii* (?)] and by bridge grafting have thus far failed."

In 1931 Guba (12) briefly described this suspected mosaic disease under the name " Gold Disease " in the annual report of the Massachusetts Agricultural Experimental Station. Recently (11) he has published an article on this disease under the name " suspected mosaic." In it evidence is cited from which he concludes that it is genetic in origin as first suggested by Berkeley (5).

In 1932 Zeller and Vaughan (18) described a disease of strawberries limited in distribution to the Pacific Coast States which they named " Crinkle." They suggested that it might be a form of virus disease but had no experimental proof of this to date. In 1933 Vaughan (19) presented evidence which demonstrated that it was a virus disease and was spread by *Myzus fragaefolii*. An interesting observation in this connection was that some of the plants apparently recovered after the first shock of inoculation. No infections were obtained by mechanical inoculations such as grafting, leaf mutilation or plant extract.

3. European Literature.

The general degeneration of strawberry stocks which followed the resuscitation of the strawberry industry after the war is well known. One of the first diseases to be identified in this period was " Red-plant." It is interesting to note that in one of the earliest descriptions (20), Wellington (1920), in dismissing the suggestion that an eelworm is the prime cause, suggests that this disease may be " a form of reversion similar to that now so common in black currants." This appears to be the earliest suggestion that a disease of the virus type may be a cause of strawberry degeneration. In 1922 Lees (21) in reviewing possible causes of Red-plant or " Patch " was unable to assign any one of those enumerated as of primary significance and stated that " a superficial view tends to the idea that the local strains are degenerating in vigour." In 1923 Turner (22) discounting the eelworm and soil hypotheses, stated that " in many respects the trouble resembles those more or less obscure diseases such as Mosaic and Leaf-roll of potato and Reversion in black currants," and emphasized the need for a careful selection of runners. Although in the same year Ballard and Peren (23) definitely assigned eelworm, *Aphelenchus fragariae*, as the main cause of Red Plant (23, 24, 26), and also of symptom groups known as " Cauliflower " and " Small leaf," Beaumont and Hodson (25) in the following year described the eelworm hypothesis as insufficient and accepted the presence of eelworm on Red-plant as a necessary factor, but suggested that its presence alone was not sufficient to produce the symptoms found.

In 1927 Briton-Jones and Staniland (30) in their investigations on the effect of aphis noted *Capitophorus fragariae* as a potential virus carrier, but, as their direct infection experiments had yielded no evidence that the disease was systemic, and as cases of recovery after the removal of the aphis had been noted, they concluded that there was no support for any virus theory in connection with this particular aphis. Further work was, however, proposed to settle this point. To the paragraph dealing with this possible aspect of aphis infestation is appended a footnote (p. 133), in which attention is drawn to the identity of the symptoms of Aphis-plant and those of Strawberry Yellows as described and figured by Plakidas (2, 4) and ascribed by him to a virus carried by an aphid. This is important in view of the close similarity of the symptoms of the American Yellows or Xanthosis and the Yellow-edge disease identified at East Malling (44).

In 1927 Ball, Mann and Staniland (29) classified the various forms of strawberry degeneration into seven groups to which causes were provisionally assigned. They did not, however, include virus among them.

In 1930 two papers were published by Massee (33, 35) on the strawberry tarsonemid mite. It may be noted that certain of the symptoms found by him to be present in case of tarsonemid attack, e.g., leaves " with the edges a sickly yellowish green " are also recorded in descriptions of other diseases, e.g., Aphis-plant, Cauliflower, Small-leaf, Patch and Yellow-edge.

Only rarely have the symptoms associated with a given causal agent been reproduced artificially under controlled conditions. In certain cases the same main causal agent is assigned to more than one symptom group, e.g., Cauliflower and Red-plant, and in all cases, with the possible exception of Aphis-plant and Mite-plant, a given group of symptoms is regarded as the result of the interaction of a number of factors rather than the action of a single pathogen. Further, the many symptom groups are found to grade into each other, so that an accurate diagnosis is often a matter of the greatest difficulty. Even when a diagnosis has been made, the assignment of a cause or causes is a debatable process and rests mainly on conjecture and observation. This situation has been admirably summarized by Hodson in a recent paper (40). However, although in certain diseases pathologists have placed the main causal emphasis on environmental conditions (soil, cultivation and climate) or on direct injury by mite, insect pests or fungus disease, the very general concurrence by workers as to the necessity of a most careful selection of parent plants for runner beds and of the rigid elimination of degenerate plants (22, 27, 34, 38, 39, 42) leads to the conclusion that the existence of an infectious principle, inherent in the plant itself, and automatically transmitted to its runner progeny, has been commonly suspected.

Strawberry diseases have lately received considerable attention in France. In a recent paper Labrousse describes 3 diseases in which Leaf-curl, Crinkle and Dwarf symptoms all play a part. He notes that they resemble the symptoms of virus diseases observed in America and considers it likely that they are induced in both cases by viruses, although so far no proof has been forthcoming in France.

Finally, the recent work in Holland by Professor Sprenger and his associates must be noted. Sprenger (37) regards the various groups of symptoms named by workers in America and Europe—Red-leaf, Red-leg, Small-leaf, Dwarf-plant, and Yellows, as probably due to the same fundamental cause. He regards this cause as being of a virus nature, and on the basis of field work he considers that the effect of these diseases on specific susceptible varieties can be reduced in a few years by the systematic selection of healthy parents. He cites three types of chlorosis and finds that his own plants fall into these categories. He regards this variation of symptoms as largely due to the superposition of the symptoms of direct insect and mite attack and virus infection.

More recently, Banga (43) working in Sprenger's laboratory on one of these forms of degeneration, describes an Actinomycete distributed throughout plants showing the typical leaf

symptoms. He notes, however, that :—"As so far no strawberry plants have been free from the *Actinomycetaceae*, no inoculation experiments could be conducted with the organism." He states his intention of attempting to raise plants free from this organism in order that such experiments can be carried out at a future date.

The difficulty (also noted by Sprenger) of determining the distinguishing symptoms of possible virus infection, due to the masking of these symptoms by those of direct mite and insect attack, convinced the present writer of the need for a method of transmission whereby the mite and insect factors could be eliminated. In 1931 various methods of grafting runners from one plant on to another were successfully attempted (44). In 1932 the same methods were applied (45) and conclusive evidence was obtained of the existence in this country of a transmissible virus-disease of strawberry plants which is clearly, apart from the direct action of associated mite and insect pests, a potent cause of the degeneration of plantations of the Royal Sovereign variety (and probably of other varieties) in Kent, and, it would appear, elsewhere in the country. In this paper (45) (p. 72) the name " Strawberry Yellow-edge " is suggested for this disease in order to distinguish it " from the disease in America referred to as Yellows (Xanthosis) (2, 4, 9) and from Mite-plants, which often show a yellow colouration of the young leaves (not localized at the leaf-edge)."

It is further emphasized that the symptoms of the disease on Royal Sovereign (a full description of which is given) are masked by insect and mite infestation and by the outdoor temperature conditions normally prevalent during the major part of the growing season. A critical diagnosis is therefore only possible when pests are adequately controlled, and on the young plants during the latter part of the season (from the middle of September to the end of October). An account is given of analogous symptoms observed on varieties other than Royal Sovereign, and of preliminary observations on apparent, relative varietal susceptibility. Finally, it is concluded that a " a system of control must aim at the elimination of virus-infected runners from runner-beds so that the grower can be confident at any stage in the career of a susceptible variety that the proportion of virus infected runners in his supply will be negligible."

At the present time experiments are in progress at East Malling to determine the natural vectors of the disease (with special reference to the possible function of the closely associated tarsonemid mite in this respect) and to devise methods of raising virus-free runners. Varietal and " strain " susceptibility to Yellow-edge is also being studied in greater detail. Certain preliminary crosses of resistant and susceptible varieties have indicated that it may be possible to manipulate " qualities of resistance " by breeding methods, and further experiments are in progress to test this point. Since the discovery of the Yellow-edge disease it has also been possible to study the occurrence and inheritance of this disease on known and recorded families, and evidence has been obtained that certain of the clone races are more susceptible than others to outside infection.

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III. THE PHENOMENON OF ROOT ROTS IN CONNECTION WITH STRAWBERRY DEGENERATION.

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Our present knowledge of strawberry troubles, both from the pomological and pathological standpoint, is not sufficiently advanced to allow us to evaluate with any degree of certainty the respective importance of the various troubles connected with degeneration. There is, however, a tendency to consider ' virus ' diseases of one kind or another as the main factor in degeneration. There is very good reason for this view, in that ' virus ' troubles have been demonstrated to play a leading rôle in the degeneration of other crops, for instance potatoes and raspberries,—and therefore it is only reasonable to expect that the same may be true for strawberries. However, we must not overlook the fact that considerable evidence has already been brought forward which points out that ' root rots ' play no small part in the deterioration of strawberries. The respective importance of ' root rots ' on the one hand and ' virus diseases ' on the other has still to be ascertained, but certain it is that ' root rots ' must at least be given serious consideration. For instance, from the standpoint of control it will avail little, even though special precautions may have been taken to secure stock free from virus diseases, if such stock after planting is to fall a prey to parasitic organisms in the soil.

Therefore at this stage of our knowledge it would seem advisable to point out that abnormalities of the roots, as well as of crown and above ground parts, must be considered in any approach to the problem of degeneration of strawberries.

One other fact that should be stressed at this time is that degeneration of the strawberry in the general sense is hardly to be put down to any one factor, but rather to a complexity of factors of which cultural practices, varietal strains, insects, general atmospheric and soil environment play their parts in addition to specific diseases, whether they be ' virus ' or ' fungous ' in nature.

In discussing ' root rot ' of the strawberry it should be clearly pointed out (1) that, although numerous references occur in literature relating to fungi or bacteria having been isolated from strawberry roots, yet in only a few instances have these fungi been proved to be parasitic, and (2) that the term ' root rot ' is used in the general sense to designate an unhealthy or rotten condition of the roots irrespective of the causal organism or organisms concerned.

The symptoms of ' root rot ' or ' black root ' as it is understood in the U.S.A. and Canada have been well described by Strong and Strong (22) and Walker (26) respectively. In giving a description of the disease Strong and Strong say " a diseased plant shows low vitality, is usually stunted and has a tendency to dry up at the onset of dry-weather conditions. Such a plant on being dug up, is found to have a root system in which the roots are all black, corky in texture and apparently dead." If, on the other hand, a plant recently affected be examined it will be found that " some of the main roots will be rotted their entire length and brown to black.—From few to many lesions are to be found on the main roots and many or all of the laterals or secondary roots will either be rotted away or show distinct rotted areas." It is by means of these lesions that this trouble can be readily diagnosed. Strong and Strong (22) give a detailed report of the disease as it occurs in Michigan, U.S.A., and record inoculation experiments which demonstrate that two fungi, *Leptosphaeria coniothyrium* (Fckl) Sacc. and *Pezizella lythri* (Desm), Shear and Dodge are capable of producing the disease. They describe the symptoms in some detail, and also record its distribution and importance. A similar disease was reported in Canada by Berkeley (5, 6, 7, 8) in 1924, and though inoculation tests were carried out with the organisms isolated from diseased roots, no positive results were obtained. Later, however, Walker (25, 26, 27, 28) demonstrated that the disease under Canadian conditions was caused by a species of *Ramularia*. Indications that a species of *Fusarium* was slightly pathogenic were also obtained.

In 1930 Plakidas (19) isolated from diseased strawberry roots in Louisiana several unidentified species of *Pythium*, one of which proved to be strongly pathogenic.

In 1932 Zeller (31) described a strawberry root disease in Oregon, and demonstrated that *Rhizoctonia Solani* Kühn was the cause. The symptoms of this root rot are quite similar to the ' black root ' disease reported by Strong and Strong (22) for Michigan, U.S.A., and Walker (25) for Ontario, Canada, though the respective causal agents are quite different.

In Scotland, Wardlaw (29) in 1926 described a trouble of strawberries associated with the so-called ' Lanarkshire disease ' with symptoms somewhat similar to ' black root.' He isolated a *Pythium* and an unidentified member of the *Fungi Imperfecti* that, upon inoculation, produced symptoms typical of the disease. He suggested, however, that unfavourable environment was most likely the primary cause, fungi being secondary. Later (30) he stated that " the problem appears to be an agricultural rather than a mycological one." His conception, therefore, was that fungi were secondary.

In England, Small (21) in 1925, working with strawberries grown under glass, reports a disease on strawberries that has somewhat similar symptoms to those associated with root rot. Inoculations showed that a strain of *Diplodina*, probably *D. lycopersici* was pathogenic.

In addition to the above reports of ' root rot ' where pathogenicity of a fungus or fungi has been demonstrated, the following cases of what appears to be the same or at least a very similar disease, though no proof of pathogenicity has been established, have been reported. Neal (17) reported a ' root rot ' of strawberries as being of importance in Mississippi in 1923, and stated that the plants wilted and the roots were discoloured. He isolated a species of *Fusarium* from effected crowns, but did not prove its pathogenicity. Sherbakoff (20) reported ' black root ' as being of some importance in the southern states in 1924. He isolated a sterile fungus from diseased roots. Coons (12) in 1924 described ' black root ' as he found it in Michigan and stated that the condition of the roots and other types of infection suggested the cause as being due to species of *Rhizoctonia*. Frank (13) reported ' root rot ' in Washington and also suspected *Rhizoctonia* as a possible cause. Heald (14) likewise reported a *Rhizoctonia* infecting strawberries at Washington in 1919. Adams and Prescott (1) report a ' plant failure ' in Victoria, Australia, and associate *Pythium* sp., *Rhizoctonia* sp. and *Botrytis* sp. with the disease, though they say " at this stage . . . . we are inclined to think that some soil deficiency may be playing an important part in bringing about this diseased condition, and that fungi are of secondary importance." Thomas (23) working in New York, had apparently much the same conception of the problem as Adams and Prescott, because he concluded that root killing may be caused by many factors and that fungi most likely play a minor rôle. Labrousse (15) working in France, recently reported an 'Apoplexie du Fraisier ' and associates *Rhizoctonia Solani*, and *Pythium* sp. as being connected with the trouble. In 1927 Ball, Mann and Staniland (4) described " sudden wilt " of strawberry but though various fungi were isolated from affected plants, no proof of pathogenicity was obtained. In a previous paper Mann and Ball (16) mention " brownish regions on affected roots." They suspected that these " brownish regions " might be caused by fungi but they considered the importance of such fungi as being practically negligible.

To summarize the situation a species of *Rhizoctonia* has been considered responsible for, or has been associated with, a root rot (black root) condition of strawberries in Michigan (Coons), Washington (Heald, Frank), New York (Thomas), Oregon (Zeller), Utah* (Blood), Australia (Adams and Prescott) and France (Labrousse). On the other hand a similar black root condition has been assigned to or associated with *Lepthosphaeria coniothyrium* (Fckl) Sacc. and *Pezizella lythri* (Desm.) Shear and Dodge [Michigan (Strong and Strong)] ; *Ramularia* sp. [Canada (Walker)] ; *Fusarium* sp. [Mississippi, U.S.A. (Neal)] ; *Pythium* sp. [Australia (Adams and Prescott), France (Labrousse), Scotland (Wardlaw) and Louisiana, U.S.A. (Plakidas)] ; and *Diplodina* sp. [England (Small)] ; a sterile fungus (Sherbakoff) and an unidentified member of *Fungi Imperfecti* (Wardlaw).

*Utah is referred to in Zeller's paper, see paper No. 31 of Bibliography.

Four other closely related diseases have been reported that must be considered separately from the above ' black root ' diseases, namely *Verticillium* wilt as described by Thomas (24), the Lanarkshire disease described by Mrs. Alcock (2), Alcock, Howells and Foister (3) and O'Brien and McNaughton (18), a crown rot caused by *Colletotrichum fragariae*, and a ' root rot ' described by Brooks and Nolan (10) as being caused by *Sclerotium Rolfsii* Sacc. Brooks and Nolen (10) also mention that they isolated three bacterial organisms which produced decay of roots under controlled conditions. It is true that the above ground symptoms of these diseases may be quite similar to those produced by ' black root,' but according to Thomas (24) there are no lesions associated with roots affected with *Verticillium* wilt, and the ' red core ' described by Mrs. Alcock (2, 3), is absent in ' black root.' Also the crown rot reported by Brooks (11) as being caused by *Colletotrichum fragariae* is primarily a rhizome rot, not a root rot, though the roots may be attacked as well. Finally, the root disease mentioned by Brooks and Nolen (10) and assigned to *Sclerotium Rolfsii* Sacc. attacks not only the roots but the rhizome, crown and fruit as well, which places it also in a different category.

Thomas (24) points out in connection with *Verticillium* wilt that the fungus responsible does not alter the external appearance of the roots, as is the case with ' black root,' and in fact suggests that the fungus is largely confined to the crown, since isolations from the roots for the most part give negative results. He pointed out the similarity of many of the ' wilt ' symptoms with those of ' black root ' or ' root rot ' and suggested that some of these diseases may have a common origin.

The Lanarkshire disease of strawberries is most likely, as Mrs. Alcock points out, not a single disease but a " congeries of diseases " of which the *Phytophthora* root rot described by her is merely one. Mrs. Alcock (2) has presented evidence to support her contention that a species of *Phytophthora* is responsible for the ' red core ' disease. Although she has, as yet, been unable to obtain the *Phytophthora* in pure culture, she has, however, been able to produce the disease repeatedly by adding portions of diseased root tips to sterile soil in which healthy ' runner ' plants were growing. Similar ' runners ' in identical soil, to which no diseased root tips were added, remained healthy.

The disease described by O'Brien and McNaughton (18) as the ' Lanarkshire disease ' and assigned by them to an endotrophic mycorrhiza may not be the same as the *Phytophthora* root rot, because they do not mention the ' red core ' which Mrs. Alcock considers a diagnostic feature of the *Phytophthora* disease. Although O'Brien and McNaughton present circumstantial evidence to support their conception of the part played by the endotrophic mycorrhiza, nevertheless, they have not supported this evidence with experimental proof of its pathogenicity.

The strawberry wilt and rot of rhizome assigned by Brooks (11) to *Colletotrichum fragariae* is primarily a rhizome rot because he writes : " The disease progresses from the old infected runner stub into the pith and cortex of the rhizome and out into the root attached.

The foregoing discussion of the literature of ' root rots ' of strawberry clearly points out (1) that this conditions is wide spread and important and must of necessity play no small rôle in the general deterioration of the strawberry and (2) that though the symptoms of the various root rots may be quite similar the causal organisms may not necessarily be the same.

Though predisposing factors such as winter injury, drought, waterlogging, or in fact any unfavourable growing condition, may increase the severity of ' root rot ' or ' black root,' sufficient evidence has been recorded to justify the statement that the ' root rot ' condition of strawberry may be the direct result of fungus attack and may occur in any type of soil, and in plantations growing under the best cultural conditions.

Many attempts have been made by different workers to control ' black root ' or root rot by direct root immersion or sterilization but so far with but little promise of success. This phase of the problem (control) has not as yet received general attention. In the meantime, however, the control measures generally recommended are (1) crop rotation, (2) use of plants with clean white roots for planting purposes, (3) preferably to secure planting stock from plantations where

' black root ' is not a factor. It is obvious that the breeding of a resistant variety will offer possibly the best means of control to a fungous root rot of this type.

Until recently ' root rot ' has received but little attention in England. That it is a factor that must be taken into consideration is now being realized, however, and a start has been made to study its effect on strawberry cultivation in England. Berkeley (9) working at East Malling has already established the fact that ' root rot ' of the ' black root ' type is present in Kent and Sussex, and that a species of *Coniothyrium* is associated with it. The diseased condition—lesioned roots and dwarfed leaves and petioles—has been repeatedly produced by inoculating healthy runner plants growing in sterilized soil with pure cultures of *Coniothyrium* sp. Field observations also point out that a ' root rot ' condition may be fairly widespread in other parts of England as well.

There appears to be good reason to believe, therefore, that ' root rot ' may be found to play a considerable rôle in the deterioration of strawberries in England, as it has been shown to do in parts of Canada and U.S.A.

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IV. THE INSECTS AND OTHER ANIMALS ASSOCIATED WITH DEGENERATION OF THE STRAWBERRY.

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Introduction.

A study of the insect pests and allied forms of the cultivated strawberry has been the subject of investigation in this country and other parts of the world for many years past.

A large number of insects, not to mention mites and eelworms have been noted, and in some instances the damage caused by these various pests is very serious, while in others the direct damage caused by them is not very pronounced.

For example, the damage caused to the roots of the strawberry plant by such soil insects as the Cockchafer (*Melolontha vulgaris* F.), the Leather Jacket (*Tipula* Spp.), the Cutworms (*Agrotis* Spp.), and the larva of the Swift Moth (*Hepialus humuli* L.) is of a very distinct type. These pests feed upon the roots and also upon the crowns of the plants, very often with fatal results.

Another group of insects which infect the plants above ground level and mainly attack the foliage are the various species of Aphides, Leafhoppers, several species of Lepidopterous larvae, Froghoppers, a species of White Fly, and three or four species of mites. These pests often cause severe damage, especially when the season is suitable for their production, and it is not uncommon to find more than one species present on a single plant.

A third group of insects attack the fruits or the flowers of the strawberry, and these pests are represented by certain *Coleoptera* which are contained in the genera *Rhynchites*, *Anthonomus*, and the family *Carabidae*.

While it is obvious that all these pests can play an important part in the economy of the strawberry plant, it would seem superfluous to refer to them all in this resumé, and only those which have been shown to be associated directly or indirectly with the actual degeneration of the strawberry will be dealt with here.

Eelworms, Insects, and Mites as possible causes of the Degeneration of the Strawberry Plant.

A good deal of literature has been published by the Pomologists and Plant Pathologists in relation to the causes of the degeneration of the strawberry plant. In this respect the Entomologist has not been left behind. As long ago as 1889 Ormerod made a study of the pests which infest the strawberry plant, and in her handbook entitled *Orchard and Bush Fruit Insects*, published in 1898, an interesting account is given of an attack of eelworms in a strawberry plantation situated at St. Paul's Cray, Kent. The plantation was noted to be in a very degenerated condition some years previously, and Ormerod found eelworms in the majority of the diseased plants. Since that period other well known authorities have studied the problem of strawberry degeneration from the entomological point of view, and a species of eelworm, several species of aphides and a species of mite have been found to be associated with some of the major strawberry problems.

For convenience it is proposed to deal with each of these three groups of animals under separate headings.

(1) The Association of Eelworm with Strawberry Degeneration.

A species of eelworm was found to be associated with the roots and crowns of strawberry plants by Ormerod (1), and a detailed description of the damage caused by the eelworm, together with notes on the life-cycle of the pest were described by her in 1898. Ormerod noted that the attacked plants showed very peculiar symptoms, and when the infestation proved to be very severe, these plants could be best compared with a piece of cauliflower; and thus the disease

which was considered to be caused by the eelworm was described as the " Cauliflower Disease of Strawberry Plants."

At that time the species of eelworm concerned was not known, and therefore specimens were forwarded to Dr. Ritzema Bos, of Amsterdam, Holland, who was a noted authority on the group. The species proved to be new to Science, and was described by Ritzema Bos as *Aphelenchus fragariae,* Ritz. Bos (2).

In 1906 Theobald (3) examined some strawberry plants which were sent to him from North Kent and he considered that the disease, which he described as the cauliflower disease of Ormerod, was caused by the same eelworm.

In three later reports (4, 5 and 6) Theobald also refers to strawberry plants being attacked by eelworms, and he states, " The appearance of the plant at once gives us a clue to the disease, the flower heads especially becoming bunched and malformed, and the stems thickened."

Theobald (7) also describes the damage caused by two species of eelworms to strawberry plants in his work entitled Insect Pests of Fruit. The two species concerned are *Aphelenchus fragariae,* Ritz. Bos, and *Tylenchus devastatrix,* Kuhn. Referring to the damage caused by *A. fragariae,* Ritz. Bos, he states that " the worms breed and reproduce in the plants. The main stem of the plant grows up, but suddenly branches vigorously, and these branches remain united in a mass, and this mass thickens like a piece of cauliflower." When describing symptoms of the damage caused by *T. devastatrix,* Kuhn. Theobald states, " There are no marked symptoms such as seen in the former '*A. fragariae,* Ritz. Bos,' the plants merely rot away, roots and crowns decay ; the leaves in some I have noticed become rather crinkled and deformed, and numbers shrivel and die."

More recently Ballard and Peren (8) came to the conclusion that the eelworm, *Aphelenchus fragariae,* Ritz. Bos, was the main cause of some strawberry diseases which they described as " Red Plant," " Small Leaf " and " Cauliflower." Their opinion was formed as a result of observations which showed that the eelworm was generally present upon plants showing symptoms of any of these three diseases.

Lees and Staniland (9), in their Progress Report on Red Plant of Strawberries, refer to the presence of eelworms in healthy strawberry plants, but at the same time they are of the opinion that the eelworm is in some way associated with the disease, though they suggest that its presence alone is not sufficient to account for the trouble.

In 1925 Staniland (10) made direct infections of eelworms to the strawberry plant, but the result of the inoculations were not available when the report was published.

A progress report on strawberry investigations published in the Long Ashton Report for 1927 (11) is of interest. In the section under pathology the abnormal forms of strawberry plants are grouped into seven distinct types or abnormal forms. Of these two only need be referred to here. They are type III, " Cauliflower," and type IV, " Red Plant." The report continues " Type III and IV are the well known " Cauliflower " and " Red Plant " forms, and it seems possible that they may represent different stages of the same disease. The evidence as to whether these forms result from attacks of the eelworm *Aphelenchus fragariae* is at present inconclusive."

Further experiments on the relation of strawberry eelworm to " Red Plant " and " Cauliflower " diseases of strawberries were conducted by Staniland and Swarbrick in the season 1927-28 (12). Their findings were not conclusive, for they remark that the relation between " Red Plant " and eelworm were not critically established. The chief difficulty in this type of investigation seems to be that of obtaining eelworm-free plants to commence with.

Brooks (13) described a disease of strawberry in Florida, U.S.A., which is found in all areas in that locality where strawberries are grown commercially. This disease is described as the

" Crimp " disease of strawberry and it is stated by the author to be caused by the eelworm *Aphelenchus fragariae*, Ritz. Bos. This Brooks subsequently proved by means of direct inoculation of healthy plants.

The " Crimp " disease is claimed to be identical with other diseases of strawberries which occur in America, and Brooks also suggests that it may prove to be the same as " Red Plant " which has been described by various workers in Great Britain.

It will be seen from the above survey of the literature that apart from the work of Brooks in the United States there is no direct evidence to show that the eelworm is directly responsible for any one of our major strawberry problems. However, there seems to be ample evidence to indicate that the eelworm factor may be important.

In future investigations it would appear to be essential for workers to commence all their experiments with eelworm-free plants, which might be obtained by treating the plants with hot water, or by some other means, so that direct inoculation experiments can be conducted on healthy, eelworm-free plants. In addition, further details of the life-cycle of the eelworm must be worked out in order that control measures can be attempted if the pest proves to be a serious one.

The more correct name of the strawberry eelworm (*Aphelenchus fragariae*, Ritz. Bos) is considered to be *Aphelenchoides fragariae*, Ritz. Bos).

(2) The Association of Aphides with Strawberry Degeneration.

Several species of Aphides have been recorded upon the cultivated strawberry, and the damage caused by them to the plant is frequently confused with the damage symptoms caused by other diseases and mites.

Theobald (14) appears to have been one of the first in this country to recognize the importance of aphides and their effect upon the plant. In 1905 he described a new species, *Siphonophora fragariella*, Theo. (= *Amphorophora fragariella*, Theo.). Observations on the life-cycle of this aphid show that it overwinters on the plant in the egg stage, and it is also suggested that the whole of its life-cycle is spent on the strawberry plant. It was also observed that this particular species did not cause very much damage to the foliage or materially alter the appearance of the plant, but it was considered to have a marked effect upon the crop.

Theobald also refers to this species of aphis in the Wye Reports for 1906 and 1907 (3, 15) and he records that it causes material damage to plants growing under glass, and also that it causes considerable harm to young strawberry plants in Worcestershire, Kent and Surrey.

This aphis is also referred to again by Theobald in his Insect Pests of Fruit (7) and the Wye Report for 1913 (6), and when referring to the damage caused by the aphis he states " The aphis not only prevents many trusses from bringing their fruits to a marketable size, but many of them settle on the fruits themselves, sheltering between the fruits and the calyx." It is also suggested by Theobald that the aphis is most abundant when there is excessive and dense foliage present.

Another new species was described by Theobald in 1912 (16). The material was collected at Hounslow, Middlesex, on cultivated strawberry plants. This species was described under the name of *Macrosiphum rogersii*, Theo. This species proved to be uncommon, and since it is of no economic importance it need not be referred to again in this report.

Yet another species of aphid was recorded by Theobald (17) from the cultivated strawberry. This species was described under the name of *Myzus fragariae*, Theo. (= *Capitophorus fragariae*), in 1912, and it was referred to by Theobald as " The Delicate Strawberry Aphis." At that time very little was known about the species, and apart from the fact that it occurred on cultivated strawberries in Middlesex and Sussex, little notice was taken of it until many years later.

In 1927 Briton Jones and Staniland (18) described some investigations they made concerning the effects of the Strawberry Aphis (*C. fragariae*, Theo.) on the strawberry plant. Their researches were probably the first made, at least in this country, on a scientific basis to determine the exact relation between the aphis and the plant. They describe in some detail the effect of the aphis attack upon the plant. This may be summarized briefly as follows :—

" (i) Crinkling of the leaf.
(ii) Occasional splitting of the leaf.
(iii) Reduction of size of the fully developed leaf.
(iv) The development of a yellowish-green tint in the leaf, particularly round the edge of the lamina.
(v) In the case of a heavy attack, serious damage to one or sometimes two of the leaflets, which may become brown and wilted and subsequently fall off, leaving only one or two leaflets instead of three.
(vi) Frequently, shortening and thickening of the petioles."

They conclude by stating that when an attack continues over a period of some two or three months " that the leaves become smaller and smaller successively as time goes on " and that the plants deteriorate into a degenerated condition. Thus it will be seen that the authors consider that the aphis is capable of causing damage to the plants, and this condition has been referred to as "Aphis Plant."

In the Long Ashton Report for 1927 (11) various types of abnormal forms of strawberry plants are described. Of these, type V is referred to as "Aphis Plant," which is said to be caused by *C. fragariae*, Theo., while type VI, which is referred to as " Patch," is thought to be caused by the aphis *C. fragariae* or to damage caused by cultural methods.

It will be seen from the above review of the literature with regard to the relation of Aphis to the strawberry plant, that more than one authority is of the opinion that at least one species, namely, *C. fragariae*, Theo., is associated with one of the forms of the degeneration of the strawberry. This may be true in certain instances but one striking fact cannot be overlooked when considering this important question. That many strawberry plantations in Kent and elsewhere " go down " into a very unhealthy condition, despite the fact that aphis has never occurred in the plantations concerned.

When considering the aphis aspect in relation to strawberry degeneration it would seem to be essential to obtain more details regarding the life-cycle and habits of the insect. Now, in spite of the considerable amount of literature on the subject very little seems to be known about the insect itself. For instance the egg stage has not been found and the question of alternative hosts has not been gone into thoroughly.

Future students interesting themselves in this work would be well advised to investigate this important aspect of the problem.

Control Measures.

Very few, if any detailed experiments have been carried out on the control of the strawberry aphides. Briton-Jones and Staniland (18) suggest that runners should be dipped, before planting in the autumn, in nicotine and soft soap. They point out that the runners should not be tied up in bundles, since the wash will not penetrate them sufficiently. In addition it is suggested that the selection of runners should be practised, since the best runners usually come from parent plants which are free from attack.

(3) The Association of Mites with Strawberry Degeneration.

Three species of mites are found on cultivated strawberries in this country, but only two of them can be considered to be of any economic importance. They are the Strawberry Tarsonemid Mite and the Strawberry Red Spider.

The Strawberry Tarsonemid Mite (*Tarsonemus fragariae*, Zimm.), was described by Zimmerman (19) in Germany as long ago as 1905, but it does not seem to have attracted the

attention of the economic entomologist until seven years later. The first economic reference appears to be that of Schøyen (20) who discovered the mite damaging strawberries in Norway in 1912, and who found that it was widely distributed in that country by 1914. This species of mite also occurs in Austria (21), Denmark (22), Sweden (23), Holland (24), Russia (25), Switzerland (26), Finland (21) and Great Britain (27).

The Strawberry Tarsonemid Mite is very widely distributed in this country. It has been reported from all the counties in the West and South of England, and it is common in the Midlands and the North. In Scotland it has been found less frequently, but it occurs in the Lothians and Lanarkshire, and it is also present in South Wales.

The Strawberry Tarsonemid Mite was first recorded in this country by Massee in 1930 (10). It was present in considerable numbers in a strawberry plantation near Maidstone. As indicated above it has been found in most parts of the British Isles since that time.

Up to the present time it has only been found on the wild and cultivated strawberry in this country. However, in other parts of Europe it has been recorded upon a number of other host plants. It has been found on the wild and cultivated strawberry in Finland and on begonia in Holland and Finland ; on raspberries in Norway ; on *Alchemellia vulgaris* in Russia ; and on pelargonium and cyclamen in Holland and Finland.

The mite has been recorded upon most of the commercial varieties of strawberries grown in England, but it appears to be more partial to the variety Royal Sovereign than other sorts. The Duke, Laxton's Noble, Stirlingworth, Stirling Castle, and Sir Joseph Paxton are often severely attacked ; while such varieties as Oberschlesien, Madam Kooi and Laxtonian frequently escape serious injury.

The symptoms of damage caused to the plants as the direct result of mite attack vary very considerably according to the variety and to the degree of the infestation. In an exceptionally dry, warm and sunny period, such as that experienced in 1933, the mites bred very rapidly, and the damage caused by them was noticeable by the middle of June, and severe mite symptoms were apparent by the middle of July. Whereas in 1932 severely mite infested plants were not seen until August or even September.

The mites feed upon the young, tender, undeveloped leaflets, and they do not live or feed upon the fully expanded leaves, unless the mite population is very large.

On established plants it is quite a simple matter to detect badly mite infested plants. The attacked leaves are very brittle, their edges tend to curl upwards, and in appearance assume a sickly yellowish-green colour. In addition many of the leaves become very distorted and crinkled. The young undeveloped leaflets often die before they expand, and frequently all the young leaflets attached to the crown of a plant turn a silvery brown colour, and some completely dry up. When this happens the plant tends to throw out new leaves which in turn are attacked and often destroyed. Under suitable conditions the mites continue to breed throughout the summer, and the damage they cause may still be going on in September and occasionally into October.

The symptoms of attack on runners are very similar to those described for the parent plant. The typical leaf crinkle is in evidence, the foliage is discoloured, and the young undeveloped leaflets turn brown and dry out. It is of importance to note that the runners become infested while still attached to the parent plant. The mites migrate along the stolons and establish themselves on the new runners as soon as they commence to grow. Thus in a suitable season, namely one suitable for rapid mite production, it is common to find the infestation so extreme that the young plants are killed outright before they have time to produce normal roots.

From observations made in the field and from experimental work carried out the writer is of the opinion that the Strawberry Tarsonemid Mite is associated with one of the causes of strawberry degeneration so commonly met with in the variety Royal Sovereign. It has been noted that some strawberry plantations may partially recover after being severely infested and damaged by mites. In other badly mite infested plantations the plants fail to recover and in practice the plants have been ploughed up.

Some details of the life-circle of the mite are described in the East Malling Research Station Report for 1932 (28), and therefore only a few points of particular interest will be referred to here. The mites live and feed most generally in sheltered parts of the plants, away from the direct sunlight. They usually occur in the folds of the young leaves which afford them ample protection. Mites of all stages and their eggs may be found on the plants from February until November, their numbers varying according to the season, and breeding is continuous all through that period. The adult female mites hibernate on the plants during the winter. At that time the mite population is at its lowest, since immature forms and eggs are not present. The females may be found tucked away in the crowns and other sheltered parts of the plants. The hibernation period extends from November until the end of February or even March.

Control Measures.

Owing to the very obscure habits of the mite it has proved to be a very difficult matter to eradicate it under field conditions.

Experiments have shown that the mite can be checked to some extent by the application of a three per cent lime-sulphur wash applied during the second week of March. The application should be repeated three weeks later if the infestation is very severe (28). This treatment, however, is not entirely efficient, and some other means of eradicating the mite from plants under field conditions has still to be worked out.

Fortunately, the same story is not true of mite infested runners. Mites can be eliminated from runners by means of the hot water treatment, a process similar to that used by bulb growers for the eradication of eelworm.

The treatment is quite simple. The runners are sterilized in warm water kept at a constant temperature of 110° F. for a period of twenty minutes. It is essential to sterilize the plants at the correct temperature, namely, 110° F., since if the temperature is allowed to reach 115° F. all the plants will be killed, conversely if the temperature falls below 108° F. the eggs of the mites are not affected.

Care must be taken to ensure that the plants do not overheat after treatment, and to avoid this it is advisable to plunge them into cold water directly they are removed from the sterilizing tank.

Further details of the hot water treatment of strawberry plants has been published recently by Hodson and Massee (29, 30).

It has been found that the hot water treatment also destroys the Strawberry Red Spider, the Strawberry Aphides, Eelworms and other pests present on the plants.

A second species of Tarsonemid mite occurs on strawberry plants in the United States and in Canada. It is a distinct species from that which is so general in many parts of Europe. The American species is *Tarsonemus pallidus*, Bks. (31), and it is closely related to the European Mite. The damage caused to the plant by *T. pallidus*, Bks., has been described by Darrow (32), and the symptoms of attack would appear to be very similar to those caused by *T. fragariae*, Zimm.

The host plants of *T. pallidus*, Bks., include the wild and cultivated strawberry, chrysanthemums, cyclamen, geraniums, antirrhinums spp, the perennial larkspur and begonias.

It is a very serious pest under glasshouse conditions and it is referred to by the name of the Pallid Mite. Although the Pallid Mite is regarded as a serious pest of strawberries in certain parts of the United States and in Canada, it is not yet established exactly how far it is connected with the main strawberry troubles which exist in those countries.

The Strawberry Red Spider (*Tetranychus telarius L.*) is the same species which infests plants under glass, and it also attacks many plants growing under natural conditions, more especially the strawberry and the hop.

The Strawberry Red Spider is far more abundant in strawberry fields than the average grower is aware of, and the damage caused by this mite is frequently very severe.

It feeds upon the under surfaces of the foliage from March until November. During the winter months the adult red spiders hibernate in the soil around the plants ; in old pieces of straw or litter ; in dead leaves, and in the crowns of the plants (33). The mites commence to feed in the spring of the year on the older leaves, and not on the young tender foliage as they might well be expected to do. They deposit their eggs on the under surfaces of the leaves from April onwards. All stages of mites and their eggs occur on the plant at any time during the growing season. The popular name of " Red Spider " is a very unfortunate choice since the mites only assume a brick red colour during the hibernation period. In their active stage their colour is pale whitish-yellow with black markings. In common with many other species of mite, the Strawberry Red Spider causes most damage to the plant in warm, dry seasons.

A red spider infested plant has its own peculiar symptoms. The red spider causes the plant to lose its natural green appearance. The foliage turns to a dull silvery green colour or even assumes a reddish hue when the attack is very severe. The leaves become somewhat malformed, they do not attain their normal size, and their texture is very " dry " and brittle. The direct effect of the Strawberry Red Spider upon the plant is not clearly understood, but it is evident that this pest must weaken the plants to some considerable extent. The fact that the Strawberry Red Spider, the Strawberry Tarsonemid Mite, the Strawberry Aphis, and the Eelworm may all occur on the plant at the same time, renders it very difficult to determine the amount of damage caused by any one of these pests.

The Strawberry Red Spider can be controlled on strawberry runners by means of the hot water treatment which is now used extensively for the control of the Strawberry Tarsonemid Mite.

This pest can be checked to a large extent by burning over the straw or litter in established fields as soon as picking has been completed.

The Association of Insects and Mites with Virus Diseases of Strawberry.

Very little research work has been carried out in England to determine whether any of the common strawberry pests are the vectors of diseases of a virus nature.

In 1927 Briton-Jones and Staniland (18) considered the possibility of the Strawberry Aphis (*Capitophorus fragariae*, Theo.) being a virus carrier. However, their experiments were of a preliminary nature, and they did not obtain any evidence to support the theory that a virus was present on the material they used. They conclude their remarks by stating " These observations lend no support to any virus theory with this particular aphis."

In 1931 the present writer started a series of experiments, which are still being continued, to determine whether either the Strawberry Tarsonemid Mite or the Strawberry Aphis are associated in any way with the virus disease of strawberry which occurs in this country, and recently described by Harris (34) and referred to by him as the " Yellow Edge " Disease of the Strawberry.

In this experiment aphids and mites were reared on healthy and virus plants. The progeny from these insects and mites were transferred to some hundred and twenty Royal Soveriegn plants which had been selected for their healthy appearance and vigorous habits.

The plants were divided up into five groups and the following inoculations were made.

Thirty plants were inoculated with mites from diseased plants. Thirty with mites from healthy plants ; thirty with aphids from diseased plants, and thirty with aphids from healthy plants. The remaining sixty plants were retained as controls.

A recent survey of these plants shows that eleven of the hundred and eighty plants exhibit distinct virus characteristics which may be summarized as follows :—

(1) Two of the plants inoculated with mites from diseased plants have produced virus symptoms.

(2) One of the plants inoculated with mites from healthy plants has produced virus symptoms.

(3) One of the control plants shows typical virus symptoms.

(4) Three of the plants inoculated with aphids from healthy plants have produced virus symptoms.

(5) Four of the plants inoculated with aphids from diseased plants show typical virus symptoms.

It will be seen from the above summary there is as yet very little evidence to show that either the mite or the aphis is a vector of the virus " Yellow Edge " disease. However, it is possible that the virus disease may exhibit itself on some more plants next year. There is a very striking difference in appearance between the control plants and those inoculated with the mites and aphids, and even if this investigation does not prove that the mites and aphids are vectors of the virus, it has clearly proved that both of them have had a very material effect upon the inoculated plants.

The fact that both mites and aphids are frequently found in the same plantation where the virus " Yellow Edge " disease is rampant tends to suggest that there may be some association between them, and experiments are being continued on a more intensive scale.

In 1925 Plakidas (35) referred to an obscure disease of the strawberry in California and he suggested that the Red Spider (*Tetranychus telarius L.*) and the Strawberry Aphis (*Myzus fragaefolii*) were strongly suspected of being the carriers of the disease.

In a further report published in 1927 Plakidas (36) states that the Strawberry Xanthosis (Yellows) is an insect borne disease, the vector in this case being the Strawberry Aphid (*Myzus fragaefolii*, Ckll.). In the same paper Plakidas states that Red Spider is not capable of transmitting Xanthosis.

A preliminary report, entitled Strawberry Dwarf, was published by Plakidas in 1928 (37). Strawberry Dwarf was considered by Plakidas to be of a virus nature, and it suggested that a species of aphid may prove to a vector. The aphis in question is probably *Aphis forbesi* Weed. In the course of a preliminary experiment this aphid transmitted the virus, but the number of plants used was not sufficient to form any definite conclusions.

Zeller (38) has also demonstrated that another disease of the strawberry, namely, Witches' Broom of strawberry can be transmitted from one plant to another by the aphid *Myzus fragaefolii*.

More recently Vaughan (39) has found that the crinkle disease of strawberry is transmitted by the aphid *Myzus fragaefolii* Ckll. Thus this species of aphid has been shown to be the vector of three diseases, namely, " Yellows," " Witches' Broom " and the " Crinkle Disease."

It will be seen from the above account that while certain insects have been found to be vectors of virus diseases in the United States there is at present no evidence to show that the same phenomenon occurs in this country. However, there is some ground to suggest that there may be some association, and work along these lines should be continued.

An important paper was published by Hottes and Frison (40) in 1931. In this article they consider that *Myzus fragariae*, Theo. (=*Capitophorus fragariae*, Theo.), the English species described by Theobald, and *Capitophorus fragaefolii*, Ckll. (=*Myzus fragaefolii*, Ckll.), the American species described by Cockerell, are the same species, and that the name *Capitophorus fragaefolii*, Ckll., is the correct one.

More recently Hille Ris Lambers (41), an authority on the Aphididae, has considered the question of the correct determination of the English and American species of the Strawberry Aphid, and he too agrees that the two species are actually the same. He states, however, that the name *Capitophorus fragariae*, Theo., and *Capitophorus fragaefolii*, Ckll., are both merely synonyms of a species described by Walker by the name of *Pentatrichopus potentillae*, Wlk. Thus, Hill Ris Lambers considers that the correct name of the English and American species is *Pentatrichopus potentillae*, Wlk.

The fact that the English and American species are the same makes it imperative to continue experiments in this country to determine whether the strawberry aphis is a vector of the virus disease " Yellow Edge." This aspect is especially important since Plakidas has shown that this aphis is a vector of a virus disease in the United States. In addition, it may be proved eventually that the English and American virus disease of the strawberry are one and the same disease. The symptoms of the two diseases appear to be very similar according to published accounts.

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